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Review article

Seed dormancy: an update on terminology, physiological genetics, and quantitative trait loci regulating germinability

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Dormancy is a form of developmental arrest and is an adaptive trait that promotes the survival of many organisms. In flowering plants, dormancy occurs in seeds and vegetative propagules (Lang 1996). Seed dormancy increases the distribution of germination over time, thus enhancing the survival of plants in an ever-changing environment. Seed dormancy is of intrinsic interest to weed scientists because it is one of 12 adaptive characteristics associated with weeds (Baker 1974). The sporadic emergence of seedlings derived from populations of dormant and nondormant weed seeds in the soil (Benech-Arnold et al. 2000; Forcella et al. 2000) is a key factor that dictates the need to apply weed control measures repeatedly within, between, and across growing seasons. My objective in writing this paper is to provide weed scientists, advanced students, and others with limited background information, some recent findings concerning the physiological genetics of dormancy, and steps toward identifying genes that directly regulate seed dormancy and germination. Molecular aspects of dormancy and germination will not be covered here because they have been reviewed recently (Bewley 1997; Li and Foley 1997). Readers can obtain additional and more extensive information on the biology and ecology of seed dormancy and germination from several recent books and reviews (Baskin and Baskin 1998; Benech-Arnold et al. 2000; Bewley and Black 1994; Casal and Sánchez 1998; Cohn 1996, 1998; Fennell 1999; Forcella et al. 2000; Hilhorst 1995, 1998; Hilhorst and Toorop 1997; Kelley et al. 1992; Kigel and Galili 1995; Simpson 1990; Vleeshouwers et al. 1995).

Definitions

Seed dormancy is the temporary failure of a viable seed to germinate, after a specific length of time and in a particular set of environmental conditions that allow germination after the restrictive state has been terminated by either natural or artificial conditions (Simpson 1990). The term quiescence is sometimes used incorrectly for dormancy. Quiescent seeds are fully germinable, but do not complete the germination process because of limiting external conditions such as light, temperature, oxygen, or moisture (Figure 1).

The term used to describe the transition of dormant seeds to a more readily germinable state is afterripening. Afterripening is loss of the dormant state over some period of time through exposure of the seeds to a set of environmental conditions after maturation and separation from the parent plant (Simpson 1990). Environmental conditions that facilitate afterripening vary with species. For example, rice and red rice (*Oryza sativa* L.) and wild oat (*Avena fatua* L.) and winter wild oat (*A. ludoviciana* Durieu) normally require afterripening under warm, dry conditions (Leopold et al. 1988; Naylor and Simpson 1961; Quail and Carter 1969), whereas *Arabidopsis* = mouse-ear cress [*Arabidopsis thaliana* (L.) Heynh], common ragweed (*Ambrosia artemisiifolia* L.), giant ragweed (*Ambrosia trifida* L.), and green foxtail [*Setaria viridis* (L.) Beauv.] generally require cool, moist substrate conditions referred to as stratification, chilling, or moist chilling (Ballard et al. 1996; Bazzaz 1970; Koornneef and Karssen 1994; Vanden Born 1971). The relationship between temperature and seed moisture for afterripening under warm, dry conditions is well described for rice, common cocklebur (*Xanthium strumarium* L.), barley (*Hordeum vulgare* L.), and wild oat, but little is known about the underlying biophysical mechanisms (Briggs et al. 1994; Esashi et al. 1993; Foley 1994; Leopold et al. 1988).

Afterripening is not an abrupt change from a dormant to a fully germinable state. Rather, seeds in a population become more responsive to a range of conditions at which they are able to germinate and less responsive to a range of conditions that restrict germination (Baskin and Baskin 1998; Bewley and Black 1994). For example, as dormant seeds afterripen, they germinate over a progressively wider range of temperatures than before afterripening (Figure 2) and at progressively higher concentrations of chemicals, such as abscisic acid (ABA), that inhibit or delay germination (Grappin et al. 2000; Walker-Simmons 1987; Wang et al. 1994). Likewise, as dormant seeds afterripen, their responsiveness to treatments that induce germination (e.g., gibberellins [GA]) progressively increases (Bianco et al. 1994; Derkx and Karssen 1993b; Garello and Le Page-Degivry 1999; Hilhorst and Karssen 1992; Karssen et al. 1989; Schuurink et al. 1992). The term "aging" is sometimes used incorrectly to describe afterripening. Aging reduces seed viability and seedling vigor (Bewley and Black 1994), although afterripening and aging can occur under the same environmental conditions (Figure 3).

There is no direct, noninvasive way to measure the degree of dormancy or amount of afterripening a seed has undergone, although research in this area is ongoing (Bradford, personal communication; Hilhorst and Bino 1999). Thus, researchers normally compare the onset and rate of seed germination in a dormant or partially afterripened population

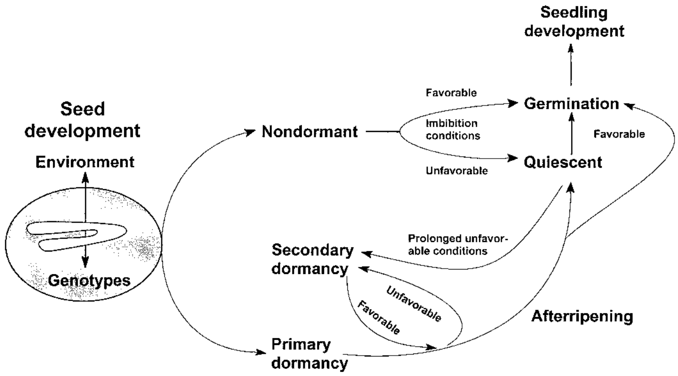

FIGURE 1. Germinability is influenced by biotic and abiotic factors from seed development through germination. During seed development, environmental and genetic factors interact to determine the level of germinability in the mature seed. After removal from the mother plant and upon imbibition under favorable conditions, mature seeds with reduced germinability are termed primary dormant. Seeds that display a relatively rapid onset and rate of germination are nondormant. Nondormant and fully afterripened seeds imbibed under unfavorable conditions normally will not germinate and are termed quiescent. Prolonged periods under unfavorable conditions for germination can result in the induction of secondary dormancy. Seeds with primary and secondary dormancy require afterripening under certain environmental conditions to achieve a state of nondormancy. Unfavorable conditions at any time during afterripening can reduce the rate of afterripening or drive the seed into a state of secondary dormancy. Annual dormancy–nondormancy cycles account for some of the periodicity of germination in the soil seedbank.

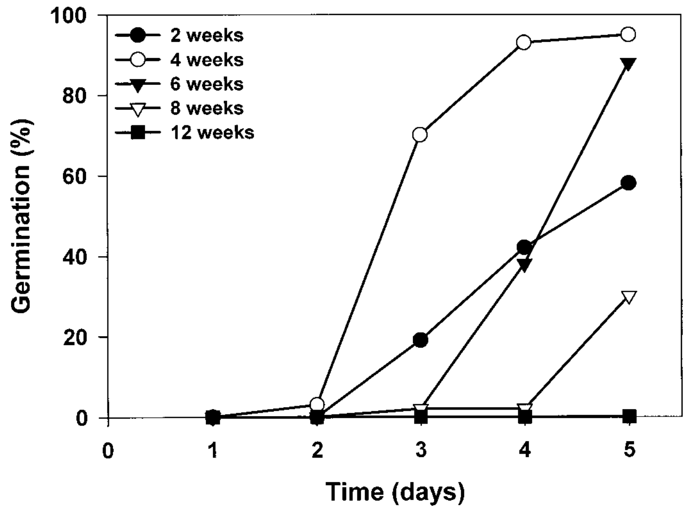

FIGURE 3. Afterripening and seed aging may occur under the same environmental conditions. Here, wild oat (*Avena fatua*) line 'M73' seeds were afterripened at 60 C and 31% relative humidity (5.2% seed moisture on a dry weight basis). Afterripening for 4 wk was required for optimum germination of the caryopses at 16 C. After 4 wk, an aging-induced decrease in seed vigor was detected, as judged by a reduced onset and rate of germination. By 12 wk, caryopses were no longer viable. See Foley (1994) for general procedures used.

with those in a nondormant or fully afterripened population under the same germination conditions (Figure 4). The dormant and afterripened seeds being compared should be from the same population or genotype if at all possible. There are pitfalls in using germination to measure the release of dormancy. Germination begins with imbibition of water by the seed and ends with the start of elongation by the embryonic axis (Bewley and Black 1994). In many environments, imbibed dormant and partially afterripened seeds will germinate after some, albeit, relatively long time. As such, how does one separate the dormancy breaking processes from the germination processes? There is evidence that something prevents the normal sequence of germination events in dormant embryos (see Cranston et al. 1999, figure 1). Until the mechanisms regulating dormancy and germination are fully elucidated, it will be difficult to separate apparently unique processes.

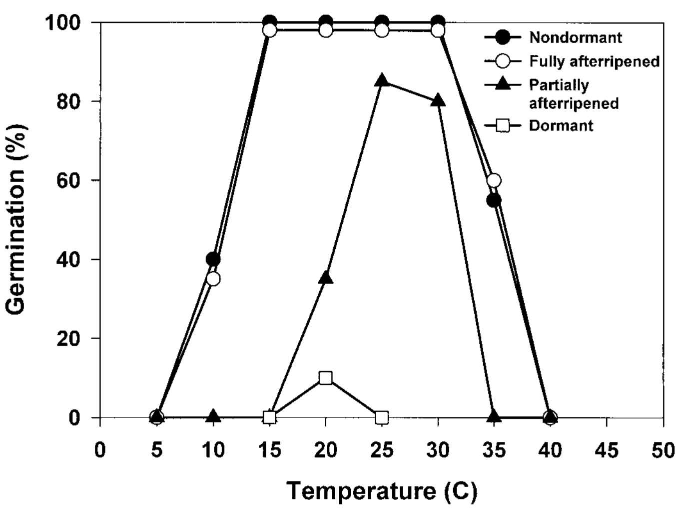

FIGURE 2. Afterripening opens up the "germination window" or allows seeds in a population to be more responsive to prevailing conditions for germination. In this hypothetical situation, seeds in various states of germinability are germinated for a fixed period (e.g., 5 d) at different temperatures. Initially nondormant and initially dormant but fully afterripened seeds germinate over a wide range of temperatures (10 to 35 C). The temperature range for germination of partially afterripened seeds is relatively reduced, and complete germination does not occur in the period of time under consideration. Dormant seeds display limited germination at 20 C.

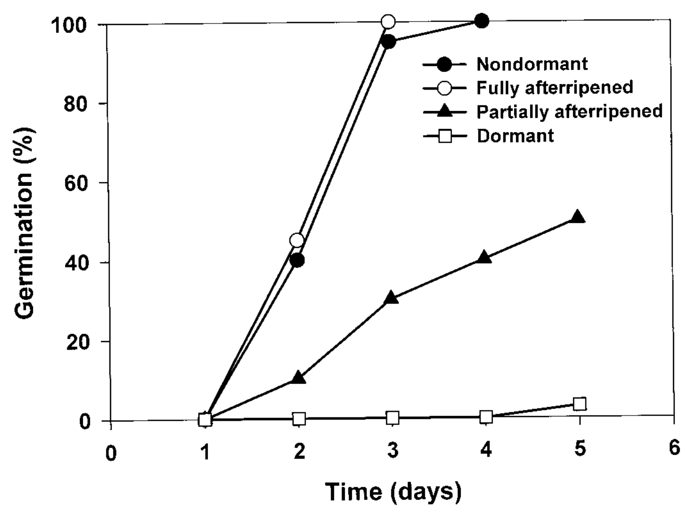

FIGURE 4. The onset and rate of germination is used to evaluate the level of dormancy or afterripening that has been attained in a seed population. In this hypothetical situation with initially nondormant and initially dormant but fully afterripened seeds of the same genotype germinated under the same conditions, the onset and rate of germination is nearly the same. The onset and rate of germination for moderately to highly dormant seeds in the population is greatly reduced compared with nondormant seeds. Often, dormant seeds will not germinate within the time period chosen to evaluate germination. The onset and rate of germination of initially dormant but partially afterripened seeds depends on the amount of afterripening that has occurred and is reduced compared with fully afterripened seeds.

Bradford (1996) outlined some common practices that lead to confounding dormancy breaking and germination processes and provided tips on experimental design and precautions to exercise in conducting research on seed dormancy. An all too common approach is to pool all seeds from a treatment—both dormant and germinated—and monitor changes sequentially over time when studying chemicals that induce germination of dormant seeds or when investigating physiological, biochemical, and molecular factors involved in dormancy. Data for parameters measured in this way are confounded. It would be best to measure the parameter on an individual seed basis. Detecting a change in an individual seed is not always practical because of limits of detection or may not be informative because of inherent variation within seeds, tissues, or cells (Still and Bradford 1997; Still et al. 1997). In lieu of measuring change on an individual seed basis, it would be appropriate to separate ungerminated from germinated seeds or embryos within a treatment at a particular time. Although this practice will eliminate some inappropriate averaging, the high level of variability, even in highly uniform seed populations, may still obscure changes that are directly or indirectly associated with germinability. Bradford and his colleagues have devised population-based threshold models that accurately quantify and predict both timing and final percent germination as they are affected by various environmental, chemical, and physiological factors (Bradford 1997; Ni and Bradford 1993). Bradford's (1996) summary of threshold modeling and experimental design and Cohn's (1996) article on important considerations for seed dormancy investigations provide some useful background information for conducting seed dormancy research.

Dormancy and afterripening are interrelated, and they are dynamic processes in the context of germination. Without knowledge about distinctive factors and mechanisms regulating dormancy and afterripening, to avoid confusion over terminology associated with these processes, some researchers have begun to use the term germinability or germination capacity (Bewley and Black 1994; Dekker et al. 1996). Dekker et al. (1996) use germinability to indicate the capacity of an embryo to germinate under any particular set of conditions. In my program, we use germinability to denote the tendency of a seed (embryo) or seeds in a population for immediate, intermediate, or much delayed germination due to internal factors, when the prevailing environmental conditions are favorable for germination of the species. The term germinability takes into account the relative nature of dormancy and afterripening as it relates to the singular event of germination. A complex interaction of internal and external biotic and abiotic factors from seed development to maturity define the tendency to germinate under a particular set of conditions at any time (Dekker et al. 1996). There is no single path leading to all germination events, and the term germinability takes this into account. For example, highly dormant wild oat caryopses that have extremely low germinability can be induced to germinate with exogenous GA in the absence of afterripening. In different ways, both afterripening and exogenous GA increased the capacity of a seed to germinate. Although both treatments increase germinability, seeds induced to germinate with exogenous GA are still "dormant," as judged by abnormal growth following germination, whereas fully afterripened seeds are nondormant (Frisby and Seeley 1993; Myers et al. 1997; Pollock 1963).

Categories and Classifications of Dormancy

Although researchers use the term germinability, they still use the terms dormancy and afterripening for practical reasons to describe, define, and clarify. Over time, many classification systems for seed dormancy have been suggested and used. Some systems are relatively comprehensive and complex (Nikolaeva 1969). Baskin and Baskin (1998) adopted Nikolaeva (1969) classification system for their comprehensive review of seed ecology. Horticulturalists frequently use the system developed by Lang et al. (1987). Other descriptive terms (e.g., photodormancy and thermodormancy) are sometimes used to classify dormancy based on a seed's response to environmental conditions that regulate germinability. For general purposes and for this review, a less complex classification system is used. This system recognizes two types and two categories of dormancy: primary and secondary dormancy, and seed coat–imposed and embryo dormancy, respectively (Bewley and Black 1994; Hilhorst 1995). The states of primary and secondary dormancy refer to the period of time when dormancy develops. Seed coat–imposed and embryo dormancy refer to the mechanisms or location of constraints to germination.

Primary dormancy refers to arrested germination of mature, fully imbibed seeds (Figure 1). Using the general-purpose classification system and this definition, seeds with immature embryos would not be considered dormant. Secondary dormancy generally occurs when dispersed, mature seeds are exposed for certain periods to environmental conditions that induce a quiescent state (Bewley and Black 1994). Not all quiescent seeds become secondarily dormant. Secondary dormancy may occur in nondormant seeds after maturation and dispersal or in partially or fully afterripened seeds. Secondary dormancy can also be induced in some seeds with inhibitors of gibberellin biosynthesis (Khan 1994). Induction of secondary dormancy in some regards is the opposite of afterripening because the range of suitable conditions for germination is decreased (Baskin and Baskin 1998, table 4.3). Generally, secondarily dormant seeds respond to the same afterripening conditions and other treatments that induce germination of primarily dormant seeds (Karssen 1982). For example, both primarily and secondarily dormant wild oat seeds respond to afterripening under warm, dry conditions (Symons et al. 1987; Tilsner and Upadhyaya 1985). Both primarily and secondarily dormant giant ragweed and common ragweed seeds respond to stratification (Bazzaz 1970; Davis 1930).

Secondary dormancy is of great interest to weed ecologists because it accounts for the annual dormancy cycles in the soil seedbank (Baskin and Baskin 1985; Benech-Arnold and Sánchez 1995; Egley 1995; Forcella et al. 1997, 2000; Karssen 1982). In contrast with primary dormancy, studies of secondary dormancy have been limited and are mostly descriptive rather than mechanistic in nature. Fundamental investigations of primary dormancy have exceeded those of secondary dormancy for several reasons. Many of the model systems used to investigate dormancy are domesticated species in which annual dormancy cycling is not an issue, as it is in weed seeds. Also, the induction of secondary dormancy sometimes requires time-consuming and tedious steps, as in the case of wild oat and cucumber (*Cucumis sativus* L.) (Hay and Cumming 1959; Sreenivasulu and Amritphale 2000). To date, there is no evidence that mechanisms regulating primary and secondary dormancy differ. In fact, several investigators have proposed rational models suggesting similar mechanisms regulate primary and secondary dormancy (Hilhorst 1998; Trewavas 1988). In the remainder of this review, I will focus on germinability as it relates to primary dormancy. In context with the classification system used by Baskin and Baskin (1998), I will focus mostly on endogenous dormancy of the nondeep and intermediate physiological types.

Seed Development and Structure

Some background information on seed development and structure is helpful to understand various aspects of coat-imposed and embryo dormancy. Consulting an introductory textbook on seeds or botany will provide some useful information beyond that provided here. As they relate to seed dormancy, we are mostly concerned with the embryo, endosperm, perisperm, testa, pericarp, and hull (lemma and palea). Sometimes the terms seed coat and fruit coat are used in lieu of testa and pericarp, respectively. Individual species may lack one or more of these tissues or structures, and their prominence and proximity to the embryo varies tremendously.

A developed embryo is comprised of the embryonic axis and one or more cotyledons. The one much-reduced cotyledon in members of the Poaceae (grass family) is referred to as the scutellum. The embryonic axis expands upon germination. Cotyledons in many dicotyledonous species contain stored food for germination. In a few species (e.g., coffee [*Coffea arabica* L.], beets [*Beta* spp.]) the perisperm serves as food storage tissue. The endosperm serves the same function in grasses and in other species with limited cotyledonary reserves. It is expedient to consider all tissues and structures adjacent to or surrounding the embryo as "covering layers." This includes the perisperm, testa, pericarp, hull, and endosperm. In grass seeds like wild oat, the endosperm is adjacent to the scutellum, whereas in leafy spurge (*Euphorbia esula* L.), the endosperm surrounds the embryo (Carmichael and Selbo 1999; Morrison and Dushnicky 1982). The prominent outer covering structure can be either the testa or pericarp or, in the case of many grasses, the hull. After the hull is removed from grass seeds, the remaining unit is the caryopsis or grain. The testa can be of considerable importance if the embryo lacks a pericarp or other tissues for protection. Maternal origin and the genetic make-up of covering layers should be considered when investigating germinability because these factors can directly influence result and hence conclusion (Dekker et al. 1996).

Coat-Imposed and Embryo Dormancy

Dormancy can be imposed upon the seed by the coat, factors within the embryo, or both. Coat-imposed dormancy is most prevalent among plant species, although embryo dormancy has been well documented in wild oat and sunflower (*Helianthus annuus* L.) (Foley 1992; Le Page-Degivry et al. 1990; Naylor and Simpson 1961). Some wild oat lines (e.g., 'M73') have both coat-imposed and embryo dormancy (Foley 1992; Naylor and Simpson 1961). The degree of dormancy imposed by the coat and the embryo varies tremendously within and among species. Hard seededness is a relatively absolute form of coat-imposed dormancy due to the impermeability of covering structures to water and/or gases. Hard seeds generally require physical or chemical scarification, boiling in water, or stratification or weathering in the soil to facilitate germination. Hard seededness is apparent in many weeds, including velvetleaf [*Abutilon theophrasti* (L.) Medicus], field bindweed (*Convolvulus arvensis* L.), purple sesbania [*Sesbania punicea* (Cav.) Benth.], and prickly sida (*Sida spinosa* L.) (Cardina and Sparrow 1997; Egley et al. 1986; Riggio Bevilacqua et al. 1987). Hard seededness is a form of dormancy for which fundamental research has been limited. Therefore, I will focus on coat-imposed dormancy that is directed by mechanisms other than hard seededness. Seed covering structures and dormancy in hard seeds has been reviewed by Egley (1989) and Kelly et al. (1992).

Physiological Genetics of *Arabidopsis* Mutants

Background

Prior to the early 1980s, the onset, control, and termination of dormancy was thought to be controlled by a balance between growth-inhibiting and growth-promoting substances (Amen 1968). Inhibition and promotion of germination was often attributed to a direct balance between the hormones ABA and GA, respectively. Environmental factors like temperature, light, and oxygen were thought to influence germinability by causing changes in the balance between inhibitors and promoters. However, insufficient and inconsistent experimental evidence, based in part on experiments with *Arabidopsis* GA- and ABA-deficient mutants (Hilhorst and Karssen 1992; Karssen et al. 1983; Koornneef and van der Veen 1980), led Karssen and Lacka (1986) to revise the hormone balance theory of seed dormancy. They postulated that embryonic levels of ABA during seed development imposed dormancy and dictated the subsequent requirement for GA during germination of seeds with coat-imposed dormancy. The hormone balance theory is still invoked to explain vivipary (precocious germination during seed development prior to maturation drying) and dormancy in some species (Steinbach et al. 1997; White et al. 2000). Vivipary can occur while seeds are still attached to the mother plant or when some developing seeds or embryos are cultured in vitro. It seems unlikely that dormancy induction during seed development is the main mechanism for the prevention of precocious germination because vivipary is not a general phenomenon in most nondormant seeds.

Because of its short life cycle, well-characterized genome, and abundant genetic stocks, *Arabidopsis* has contributed greatly to knowledge of seed development, dormancy, and germination through genetic analyses and physiological characterizations (Koornneef and Karssen 1994). Mutant lines in which the biosynthesis of ABA, GA, or both is impaired or the sensitivity to one of these hormones is strongly reduced have played key roles in shaping our current knowledge and hypotheses (Koornneef and van der Veen 1980; Koornneef et al. 1982, 1984, 1985; Nambara et al. 1992). Several *Arabidopsis* mutants with altered seed morphology or response to light have provided insight into

Table 1. Generalized response of dormant (D) vs. nondormant (ND) embryos/seeds of several crops to abscisic acid (ABA) and gibberellic acid (GA) as it relates to germinability.

Characteristic	Response				References
	Wheat	Barley	Sunflower	Tobacco	
ABA in mature D embryos[a]	Higher[b]	Higher[b]	Higher[b]	Higher[b]	Bianco et al. 1994; Grappin et al. 2000; Walker-Simmons 1987; Wang et al. 1995
Sensitivity of D embryos to exogenous ABA[c]	High	High	High	High	Grappin et al. 2000; Le Page-Degivry and Garello 1992; Morris et al. 1989; van Beckum et al. 1993; Walker-Simmons 1987; Wang et al. 1994
Sensitivity of D embryos to exogenous GA[d]	—[e]	Low	Low	Low	Bianco et al. 1994; Grappin et al. 2000; Wang et al. 1994
Responsiveness of D embryos to an ABA biosynthesis inhibitor[f]	High	High	High	High	Garello and Le Page-Degivry 1999; Grappin et al. 2000; Le Page-Degivry and Garello 1992; Rasmussen et al. 1997; Wang et al. 1998
Biosynthesis of ABA in imbibed D embryos[a]	Yes	Yes	Yes	Yes	Bianco et al. 1994; Garello and Le Page-Degivry 1999; Grappin et al. 2000; Wang et al. 1995

[a] Determined biochemically.
[b] Depending on the species, levels in dormant embryos/seeds ranged from 25 to 300% higher than in the nondormant embryos/seeds.
[c] Generally determined by germination of dormant, partially afterripened, and nondormant seeds/embryos in the presence of abscisic acid (ABA).
[d] Generally determined by germination of dormant and partially afterripened seeds/embryos in the presence of increasing concentrations of gibberellin (GA).
[e] Not determined.
[f] Generally determined by germination of dormant seeds/embryos in the presence of fluridone.

the effects of seed structure, chemical composition, and phytochrome on germinability (Debeaujon et al. 2000; Léon-Kloosterziel et al. 1994; Shinomura 1997). Genetic stocks and mutants of other species, such as barley, two-row barley (*Hordeum distichum* L.), maize/corn (*Zea mays* L.), sunflower, tobacco (*Nicotiana plumbaginifolia* Viv.), tomato (*Lycopersicon esculentum* Mill.), and wheat (*Triticum aestivum* L.), that have also been important in developing knowledge of seed development and germinability will not be reviewed. However, some generalizations about the response of several species to ABA and GA have been summarized (Table 1) to complement the discussions on *Arabidopsis.* McCarty (1995) and Hilhorst (1998) have recently reviewed various aspects of seed development and germinability in maize and tomato, respectively.

Table 2. Brief guide to nomenclature rules for genes identified by mutation.[a]

1. The wild-type allele should have three capital letters written in italics or underlined (*ABC* or <u>ABC</u>). Some gene symbols chosen before these guidelines may have two letters.
2. Mutant gene symbols should have three lower case letters written in italics (*abc*).
3. The full descriptive names of the wild-type (*ALPHABETICA*) and mutant (*alphabetica*) alleles should be written in the same manner.
4. Protein products of genes should be written in capital letters without italics (ABC).
5. The phenotype is designated by the gene symbol, which is not italicized but has the first letter capitalized. Abc^{+} and Abc^{-} describe the wild type and mutant phenotype, respectively.
6. Different genes with the same symbol are distinguished by different numbers (*abc1* and *abc2*).
7. Different alleles of the same gene are distinguished with a number following a hyphen (*abc4-1* and *abc4-2*). When only a single allele is known, the hyphen is not needed. Thus *abc3* = *abc3-1* if only a single allele is known.
8. The most direct way to indicate the double mutant produced by crossing *abc1* with *xyz2* is *abc1 xyz2* double mutant.

[a] Adapted from Meinke, D. and M. Koornneef. 1997. Community standards: a new series of guidelines for plant science. Plant J. 12:247–253 and http://mutant.lse.okstate.edu/genepage/namerule.html. Last accessed January 21, 2001.

Before considering Karssen and Lacka's (1986) revised theory, it may be helpful to review genetic nomenclature (Table 2), make some generalizations about germinability, and describe afterripening of *Arabidopsis* seeds. The names of some mutants may not conform to recent guidelines. For example, the GA-deficient mutant *ga1* was named prior to implementation of the guidelines (Koornneef and van der Veen 1980). In other cases, mutants have been renamed to fit recent guidelines. For example, loci involved in GA deficiency in tomato were changed from *ga-1* and *ga-2* to *gib1* and *gib2,* respectively (Karssen et al. 1989).

As one considers germinability of wild-type and mutant seeds, it is important to keep in mind that germinability or the afterripening requirement is influenced by several factors. For example, the genetic background of the line, the specific mutant allele at a particular locus, and the environmental conditions during seed development all can affect dormancy (Derkx and Karssen 1993a; Léon-Kloosterziel et al. 1996). Different mutant alleles at a particular locus do not always affect germinability in the same way (Koornneef et al. 1982, 1985; Nambara et al. 1992). For example, if the mutant allele is weak (referred to as leaky), it may still have some capacity to function, albeit at a reduced level, whereas a strong mutant allele implies a complete loss or gain of function compared with the wild-type.

Arabidopsis seeds require stratification but also respond to afterripening under warm, dry conditions to develop their full germination capacity. Stratification increases germinability of *Arabidopsis* seeds more rapidly than afterripening under warm, dry conditions (Karssen and Lacka 1986). It is not unusual for seeds to respond to more than one type of afterripening treatment, although one type will generally have more efficacy than another in a particular species. The duration of afterripening required for full germinability depends on the line (genotype). For example, the commonly used *Arabidopsis* lines 'Columbia' (Col) and 'Landsberg *erecta*' (L*er*) require short periods of afterripening, whereas 'Wassilevskija' (Ws) and 'Cape Verde Island' (Cvi) require relatively long periods of afterripening to obtain optimum germination at room temperature (Debeaujon and Koornneef 2000; Debeaujon et al. 2000; Koornneef et al. 1999). Seeds from several *Arabidopsis* mutant lines do not require afterripening for rapid germination (Koornneef et al. 1982, 1984; Meinke et al. 1994; Nambara et al. 1991). For example, *aba* mutants have reduced or no seed dormancy and a reduced requirement for light during germination (Groot and Karssen 1992; Karssen et al. 1983; Koornneef et al. 1982). The wild-type (*ABA*) seeds are dormant and therefore require afterripening. Abscisic acid biosynthesis is inhibited in *aba* mutants; thus, they are ABA deficient.

Abscisic Acid

Dormancy is established during seed maturation, and ABA is thought to play a key role. ABA was measured in seeds from plants derived from reciprocal crosses of wild-type and several ABA-deficient mutants. These measurements demonstrated two rises in ABA during seed development. The first, sharp rise of maternally derived ABA is regulated by the genotype of the mother plant. The second, low rise in embryonic ABA is regulated by the genotype of the embryo. The onset of dormancy is correlated with the second, but not with the first rise in ABA (Karssen et al. 1983). Similar results were obtained with crosses between a wild-type and ABA-deficient mutant of tomato (Groot and Karssen 1992). The ABA level becomes very low during the late stages of maturation. Such low levels of ABA cannot account for maintenance of dormancy in imbibed wild-type seeds. Thus, the level of embryonic ABA during maturation, rather than in the dry or imbibed fully mature seed, seems to be responsible for the induction of seed dormancy (Karssen and Lacka 1986). Application of fluridone, an ABA biosynthesis inhibitor, before the developmental rise in ABA levels in sunflower seeds prevents further ABA biosynthesis and the development of embryo dormancy (Le Page-Degivry and Garello 1992). Hilhorst et al. (1998) has outlined some research that is inconsistent with Karssen and Lacka's (1986) hypothesis. For example, a correlation between the depth of dormancy and the ABA content during maturation is not always apparent.

Recent evidence that ABA biosynthesis occurs in *Arabidopsis* seeds during imbibition suggests another level at which ABA may impose or maintain dormancy (Debeaujon and Koornneef 2000). Abscisic acid biosynthesis occurs in imbibed dormant, but not nondormant, embryos of several species (Table 1). Dormant seeds and embryos of these species are significantly more sensitive to the inhibitory effects of exogenous ABA than nondormant seeds (Table 1). Afterripening reduces an embryo's capacity for ABA biosynthesis and reduces its sensitivity to exogenously applied ABA (Table 1). Fluridone application to dormant embryos also facilitates rapid germination (Table 1). Although it is not known whether afterripening treatments decrease the sensitivity of *Arabidopsis* seeds to ABA, ABA biosynthesis in relatively ABA-sensitive embryos might reduce their germinability.

Promotion of Germination by Gibberellins, Light, and Stratification

Because exogenously applied GA induces the germination of many dormant seeds in the absence of afterripening or light treatment, GA is thought to have a regulatory role in dormancy or germination. In most seeds, a high level of GA is present during seed development and decreases during maturation; thus, mature seeds contain very low levels (Karssen et al. 1989). Gibberellin levels generally remain low or increase transiently during stratification. It seems unlikely that GA plays a role in relief of dormancy, judging from this pattern of biosynthesis (Hilhorst and Karssen 1992). However, GA may be important for germination since its level increases dramatically or remains above the level in dormant seeds when stratified European filbert/hazel (*Corylus avellana* L.) seeds or afterripened wild oat seeds are transferred to germination conditions (Arias et al. 1976; Metzger 1983).

Gibberellin-deficient, GA-insensitive, and phytochrome mutants of *Arabidopsis,* and various recombinants of these mutants, have been useful in examining the role of GA, light, and chilling in dormancy breaking and germination (Derkx and Karssen 1993b; Koornneef and van der Veen 1980; Koornneef et al. 1985; Peng et al. 1997). Biosynthesis of GA is impaired in GA-deficient mutants (e.g., *ga1*). These mutants normally require exogenously applied GA for germination, although the requirement is not always absolute because some weak mutant alleles are expressed (Koornneef and van der Veen 1980). Wild-type *Arabidopsis* seeds generally require afterripening for germination, although exogenous GA can substitute for this requirement (Derkx and Karssen 1993b; Koornneef et al. 1985; Nambara et al. 1991). Exogenous GA is sometimes required for germination of afterripened wild-type seeds in darkness, whereas light allows germination of these seeds to proceed in the absence of exogenous GA (Debeaujon and Koornneef 2000; Karssen et al. 1989). The dependency on applied GA for the germination of strong *ga1* mutants and dormant wild-type seeds strongly suggests a primary role for GA in germination.

In general, afterripening treatments increase the sensitivity of most seeds to hormones, chemicals, and physical treatments (e.g., light, wounding) that promote germination (Derkx and Karssen 1993b; Hilhorst and Karssen 1988). Stratification increases the sensitivity of both *ga1* and wild-type seed to GA in darkness as judged by their responsiveness to decreased concentrations of GA. Afterripening also increases the sensitivity of dormant embryo from other seeds to GA (Table 1). Because stratification influences germinability of *Arabidopsis* GA biosynthetic mutants, dormancy relief by chilling is apparently independent of GA (Karssen et al. 1989).

Exposure to light has a dual action on the germinability of *Arabidopsis* seeds (Hilhorst and Karssen 1988; Karssen and Lacka 1986). The first stimulatory effect of light is dependent on the biosynthesis of GA since tetcyclacis, an inhibitor of GA biosynthesis, blocks this effect (Derkx and Karssen 1993b; Hilhorst and Karssen 1988). The second effect confers a lower requirement for GA and is independent of GA biosynthesis (Hilhorst and Karssen 1988). The implications of these findings are that light stimulates GA biosynthesis and simultaneously increases the seed's sensitivity to GA. Thus, stratification and light have no intrinsic regulatory role in dormancy, but they stimulate germination through increasing GA synthesis during germination and, secondarily, through enhancing the seed's sensitivity to GA (Derkx and Karssen 1993b; Derkx et al. 1994). Although it is known that stratification has more efficacy in promoting germination than light in a variety of *Arabidopsis* mutant and wild-type line seeds, the capacity of light and cold to alleviate the GA requirement depends on the genetic background. For example, in highly dormant lines such as Ws, both cold and light are required for optimum germination, whereas in the less dormant line L*er*, cold is sufficient (Debeaujon and Koornneef 2000).

Although the action of stratification may be primary to that of light, light and its effects on the photoreceptor phytochrome (Phy) have been well characterized in the photoregulation of germination (Casal and Sánchez 1998). Phytochrome consists of a family of chromophore-containing protein photoreceptors (PHYA to PHYE) and are classified into type I (labile) and type II (stable) groups on the basis of stability of the Phy far-red (P_{fr}) form (Furuya 1993). The diversity of molecular forms of Phy suggests that they may have discrete functions. PhyA is responsible for the very low fluence response (VLFR) and PhyB for the low fluence response (LFR). PhyA photoirreversibly stimulates germination of seeds with a very low fluence of irradiation of wavelengths from ultraviolet (UV)-A to far-red. The PhyB-mediated LFR reactions are photoreversible and responsive to red and far-red wavelengths of fluence four orders of magnitude higher than those to which PhyA responds (Shinomura et al. 1996). There is a major difference in the P_{fr} requirement between the two responses. The PhyA response requires an extremely low ratio of P_{fr} to total Phy, whereas the PhyB response appears to require a much higher ratio.

Arabidopsis seeds respond to photoreversible induction and inactivation of germination, and the spectral quality of light during seed development influences germinability (Hayes and Klein 1974; Shropshire et al. 1961). Investigations of germination using wild-type and mutants that are deficient in one of the molecular types of Phy has provided insight into the role of Phy in germination (Shinomura 1997). PhyA and PhyB modulate *Arabidopsis* seed germination in distinct ways. The mechanism for Phy-mediated germination of *Arabidopsis* seeds may be to transduce red-light stimuli into molecular signals that culminate in the expression of specific genes in the GA biosynthetic pathway and genes that enhance the sensitivity of seeds to GA (Derkx et al. 1994; Hilhorst and Karssen 1988; Martinez-García et al. 2000; Yamaguchi et al. 1998). The increase in active GA may promote germination by weakening seed structures that restrict radicle growth, counteract ABA-related embryo dormancy by enhancing the growth potential of the radicle, or both (Debeaujon and Koornneef 2000; Groot and Karssen 1987; Yamaguchi et al. 1998). Phytochrome seems to be a factor regulating germinability of some, but not all, weed seeds (Botto et al. 1998; Casal and Sánchez 1998; Hartmann and Nezadal 1990; Hou and Simpson 1992; Milberg et al. 2000; Taylorson 1989).

Testa Mutants

Mature *Arabidopsis* seeds are characterized by a brown testa due to condensed tannins of the procyanidin type. The testa protects the embryo and is a physical barrier to protrusion of the radicle. Several mutant lines have been identified that have altered testa pigmentation or structure. Most testa mutants have reduced seed dormancy, as judged by a shorter afterripening requirement and higher germination rate compared with the wild-type. The reduction in dormancy is more pronounced in testa pigmentation mutants than in structure mutants (Debeaujon et al. 2000). There are two main defects in the pigmentation mutants: (1) replacement of proanthocyanidin polymers with anthocyanins that leads to increased permeability and (2) reduction of phenolic impregnation of the endothelium and the crushed parenchymatic layers, which in turn reduces thickness of the testa (Debeaujon et al. 2000). Testa removal can substitute for the GA requirement for germination of *ga1* mutants and some *tt* (transparent testa) mutants germinate in the absence of stratification, light, or GA (Debeaujon and Koornneef 2000). These results and previous research provide evidence that the GA requirement for germination may be imposed by the testa.

Pigmentation of the testa as it relates to resistance to preharvest sprouting has also been investigated in several other species. Preharvest sprouting is germination in the inflorescence after maturation of the crop but before harvest, when moist conditions prevail or untimely rains occur. Resistance to preharvest sprouting is correlated with the level of dormancy in mature seeds and is quite common in some cultivars of wheat, barley, rice, sorghum [*Sorghum bicolor* (L.) Moench], and groundnut/peanut (*Arachis hypogaea* L.). Color in wheat grains is located in the testa, and red-grained wheat are more resistant to preharvest sprouting than white-grained wheat. Red grain color is dominant, with three genes on chromosome 3—A, B, and D—regulating the trait in an additive manner (Flintham 2000; Mares 1996; Paterson and Sorrells 1990; Warner et al. 2000). Traditionally, problems with preharvest sprouting in sorghum have been partially solved by growing genotypes with high tannin content in the testa (Lijavetzky et al. 2000). Testa pigmentation also regulates germinability of proso millet (*Panicum miliaceum* L.) (Khan et al. 1996).

It is clear from research on a variety of seeds that, in different ways, ABA and GA play key roles in determining seed germinability. Results from investigations on *Arabidopsis* and other species (Table 1) are generally consistent with the hypothesis that the ABA level during seed development regulates induction of seed dormancy, whereas GA are involved in germination. Recent evidence that the state of germinability may be regulated by ABA biosynthesis in imbibed, dormant embryos that are relatively sensitive and insensitive to ABA and GA, respectively, may bring us back full circle to the hormone balance theory. We should work toward a revised theory that integrates the role of ABA during development and changes in ABA and GA levels and tissue sensitivity in dormant seeds, with the effect of dormancy breaking treatments like afterripening (Bradford and Trewavas 1994; Trewavas 1988).

Quantitative Trait Loci Analysis

Mutants such as those described in the preceding sections are relatively easy to study using physiological, biochemical, and Mendelian genetic approaches because the phenotypic effects are conditioned by one major allele. Although these mutant stocks are extremely useful and common in the laboratory, they are rare in nature because most of these individuals would be eliminated by natural selection. In any event, most genetic variation for traits observed in nature is polygenic, or controlled by multiple genes (Tanksley 1993). Characteristics like seed germinability, in which phenotypic variation is continuous instead of discrete and is conditioned by allelic variation at several to many genetic loci each with a relatively small effect, are more common in nature and are referred to as quantitative traits (Jansen 1996; Tanksley 1993). A segment of the chromosome associated with the expression of an individual locus controlling a quantitative trait is referred to as quantitative trait loci (QTL) (Tanksley 1993). The discipline of quantitative genetics uses statistics to describe characteristics of quantitative traits. The quantitative nature of dormancy has been described for a number of species and some of this work has recently been reviewed (Foley and Fennimore 1998). I expect that cloning germinability QTL in *Arabidopsis* and rice will have a major effect on dormancy investigations in weedy species (see Conclusion). Some genes that are determined to regulate germinability in *Arabidopsis* and rice can be used to clone orthologous loci in agronomically important species like wild oat or in other weedy species where germinability has not been as extensively characterized. Orthologous loci are gene loci (and by extension a region containing orthologous gene loci) that arose from a common ancestor and that are conserved in different species, for example, rice and oats (*Avena* spp.) (Devos and Gale 1997; Keller and Feuillet 2000).

The advent of DNA-based molecular markers has made it possible to dissect polygenic traits into their genetic components by genetically mapping QTL (Frary et al. 2000; Paterson et al. 1988). The basis for QTL detection is an experimental population segregating for the trait of interest (e.g., early vs. late germination) and identification of the association between the genetically determined phenotype and specific genetic marker(s) (McCouch and Doerge 1995). The methodology of QTL analysis allows researchers to quantify the effects of individual loci, to investigate interactions between loci and to investigate genotype by environmental interactions. Theoretical considerations and practical steps involved in developing maps and conducting QTL analyses are beyond the scope of this review. Because such information is helpful to understand QTL analysis of germinability, readers are urged to consult comprehensible reviews by McCouch and Doerge (1995), Paterson et al. (1991), or Tanksley (1993).

Because we recently reviewed marker-assisted detection of germinability QTL for wheat and barley (Foley and Fennimore 1998), I will focus on similar approaches in wild oat, rice, and *Arabidopsis.* Wild oat and rice are monocots, and *Arabidopsis* is a dicot. Bulked segregant analysis is a method that involves comparing two pooled DNA samples of individuals from a segregating population originating from a single cross to identify molecular markers associated with a contrasting trait (Michelmore et al. 1991). We conducted bulked segregant analysis using an F_2 population and random amplified polymorphic DNA (RAPD) techniques (Williams et al. 1990) to identify molecular markers linked to QTL regulating germinability in wild oat (Fennimore et al. 1999). Two amplified loci (bands) were linked with early germination, which is conditionally the dominant form of the trait. These two markers explained only 19% of the phenotypic variation for germinability in a random F_2 population. However, because more than two QTL regulate germinability in wild oat (Fennimore et al. 1999; Jana et al. 1979), we are seeking additional and more tightly linked markers using amplified fragment length polymorphism (AFLP) techniques (Vos et al. 1996). Like RAPDs, AFLP techniques are based on the versatile polymerase chain reaction (PCR), but AFLP is the more robust technique for identification of molecular markers.

Plant breeders and geneticists are seeking molecular markers tightly linked to germinability QTL in rice, wheat, barley, and sorghum in order to conduct marker-assisted selection breeding for resistance to preharvest sprouting. Wan et al. (1997) identified isozyme markers for individual QTL regulating germinability in two populations of rice. Dormancy was linked with six markers on chromosomes 3, 6, 7, and 12. Each locus contributed 5 to 10% to the total phenotypic variance. All QTL were not detected in both populations. For example, a gene for seed dormancy linked with the isozyme marker *Pgi-1* on chromosome 3 in 'Milyang 23' was not detected in 'IR 36', whereas a gene linked with a marker on chromosome 12 in IR 36 was not detected in Milyang 23. This and similar observations illustrates an important point: Not all genes segregate in every population. Because the same set of genes do not always regulate germinability, segregating populations derived by crossing several different dormant and nondormant lines must be produced and evaluated to identify all the major and minor genes that regulate germinability within a species.

The rice varieties 'Nipponbare' and 'Kasalath' are parental lines for the populations used by the Japanese Rice Genome Research Program to construct a genetic map with a high density of molecular markers (Harushima et al. 1998). Coincidently, Nipponbare and Kasalath seeds with intact hulls display 81 and 1% germination, respectively, after imbibition for 7 d at 30 C. Therefore, Lin et al. (1998) developed a backcross inbred line population to the fifth generation (BC_1F_5) based on the original cross to identify molecular markers linked with QTL regulating germinability and the heading date of rice. Germination in the backcross population ranged from 0 to 100% and the frequency of dormant and moderately dormant families was high. This frequency supports observations that, at least in rice, dormancy is genetically the dominant form of the trait. Five QTL affecting germinability were detected on chromosomes 3, 5, 7, and 8, with two QTL on the long arm of chromosome 7. The QTL on chromosome 3 marked by the restriction fragment length polymorphisms (RFLP) probe C1488 explained about 26% of the total phenotypic variation for germinability in the backcross inbred line population, whereas the remaining QTL explained about 7 to 11%. Nipponbare alleles had an increasing effect on the germination rate, except those for the QTL on chromosome 8 (Lin et al. 1998). Most of the isozyme markers have not been extensively integrated into the DNA-based genetic map for rice (Harushima et al. 1998), so comparison of positional similarity of QTL among rice populations is problematic. However, it is known that the loci marked by C1488 (Lin et al. 1998) and *Pgi-1* (Wan et al. 1997) map to the short and long arm, respectively, of rice chromosome 3 (Harushima et al. 1998).

Unless one invokes some sort of chromosomal rearrangement, these two QTL could not represent the same gene. It is possible that one or more of the other QTL regulating germinability in these populations represent the same genetic locus. Quantitative trait loci detected across several segregating populations derived from different genotypes and cultured under a variety of environmental conditions will likely represent major regulatory genes for germinability. These QTL will be primary targets as investigators begin to clone genes regulating germinability.

Comparative linkage maps can provide the basis for comparing and interpreting genetic information from related or divergent species. The consensus comparative map developed by Devos and Gale (1997) documents that genomes of a number of monocot species (grasses) display collinearity (sometimes termed synteny), or conservation of the gene order within a chromosomal segment between different species (Keller and Feuillet 2000). It is likely that some loci underlying germinability have been conserved during periods of evolutionary divergence and domestication (Bennetzen and Freeling 1997; Paterson et al. 1995). Collinearity and conservation of gene function will be useful characteristics as molecular markers are sought, as germinability is investigated in additional plant species, and as positional cloning of these chromosomal regions is considered. Barley and wheat are closely related members of the Triticeae tribe, and several markers for germinability QTL in barley are positionally similar to germinability QTL in wheat. For example, a major QTL on barley chromosome 7 (5H) marked by PSR128 is positionally similar to a QTL on wheat chromosome 5DL marked by BCD1874 (Larson et al. 1996; Sorrells and Anderson 1996). Barley chromosome 7 is homoeologous to chromosome 5 of wheat, in that both chromosomes, although in different species, originate from a common ancestral chromosome (Keller and Feuillet 2000). Although rice and species in the Triticeae tribe are more distantly related members of the Poaceae family, a QTL for germinability on the long arm of rice chromosome 12 (Wan et al. 1997) may be orthologous to the dormancy QTL in wheat and barley marked by BCD1874 and PSR128, respectively. Positional similarity in the location of QTL in different but related taxa does not prove identity between underlying genes, but it does suggest they could represent orthologous genes.

Segregating populations used to develop genetic linkage maps can be used to identify molecular markers for germinability, provided there are sufficient heritable differences in germinability between the parents (Han et al. 1999; Lin et al. 1998). However, a different approach was initially taken by Van der Schaar et al. (1997) to identify QTL for seed dormancy in *Arabidopsis.* They used a genetic mapping population derived from the parents L*er* and Col that both had low levels of seed dormancy. The rationale for using a population derived from parents with low levels of dormancy was to determine QTL that influence germinability under different environmental conditions. Environmental conditions greatly influence germinability of *Arabidopsis* seeds (Derkx and Karssen 1993a; Léon-Kloosterziel et al. 1996). Fourteen QTL were identified from their analysis. Nine QTL were detected in all three germination environments, whereas the other five were detected only under specific germination conditions. Thus, some of the loci appear to control germinability in a general way, whereas other loci affect environmentally specific aspects of germinability.

The existence of *Arabidopsis* lines with higher levels of dormancy than those in L*er* and Col suggests that either more genes or stronger alleles at known QTL regulate germinability, including some with major effects (i.e., account for a relatively large proportion of the phenotypic variation for germinability) as seen in the grasses (Anderson et al. 1993; Lijavetzky et al. 2000; Lin et al. 1998; Oberthur et al. 1995). Maarten Koornneef and his colleagues have developed an *Arabidopsis* recombinant inbred line population by crossing the strongly dormant Cvi and less dormant L*er* accession (Alonso-Blanco et al. 1998). QTL analysis using this population identified seven chromosomal regions affecting germinability, with one region on chromosome 5 containing a major QTL. Near-isogenic lines differing only in this region have been developed and will be used for cloning this QTL in the future (Koornneef et al. 1999). These genetic stocks and the completed sequence of the *Arabidopsis* genome will greatly facilitate cloning genes that directly regulate germinability.

Cloning QTL that Directly Regulate Germinability

There is no definitive evidence that a QTL directly involved in the regulation of dormancy has been cloned. In several species, the map positions of loci for monogenic mutants or other characteristics that affect germinability are known to overlap with the position of germinability QTL (Lijavetzky et al. 2000; Sorrells and Anderson 1996; Van der Schaar et al. 1997). However, a similar map position does not mean genes for such characteristics directly coincide with the QTL. For example, the maize *Vp1* (*VIVIPAROUS1*) gene, which has a role in integrating control of germinability, does not coincide with a known germinability QTL in wheat or rice (Bailey et al. 1999; Hoecker et al. 1995; Jones et al. 1997). In barley, the major germinability QTL on chromosome 5H (Ale–ABC302 interval) coincides with a gene controlling β-glucanase malt activity. Because the state of dormancy is correlated with β-glucanase activity and endosperm cell wall breakdown, a biochemical case could be made for a single genetic determinant in this region of chromosome 5H (Han et al. 1995). However, additional research will be required to substantiate that the QTL controlling β-glucanase activity and germinability represent the same locus.

Arabidopsis is well-suited for map-based cloning of genes because of its many genetic attributes and tools. Rice is the monocot system of choice for map-based cloning of genes for many of the same reasons (Devos and Gale 2000; Han et al. 1998; McCouch and Doerge 1995; Song et al. 1995). Until recently, the effort to sequence the entire *Arabidopsis* genome (and hence clone genes) was much further along than in rice. Thus, if there was collinearity between the *Arabidopsis* and the rice genomes, then the *Arabidopsis* sequence might be used to identify candidate genes for traits in cereals and other grasses (Schmidt 2000). Although only small segments of the *Arabidopsis* and rice genomes have been compared, most reports show that conservation of gene order has been eroded over the approximately 130 to 240 million yr since the evolutionary divergence of monocots and dicots (Devos and Gale 2000). Therefore, it is unlikely that collinearity of monocots and dicots is sufficient to allow map-based, cross-species gene prediction and isolation (Devos and Gale 2000). However, this potential problem became immaterial when the Monsanto Company (now a subsidiary of Pharmacia) announced that their working draft sequence of the rice genome will be made public through the Japanese Rice Genome Research Program. This international program will combine sequence data and place all information in the public domain as soon as possible. Public access to the *Arabidopsis* and rice genome sequences will have a major effect on efforts to clone genes. The complete sequence will allow direct identification of candidate genes based on the phenotypic mapping date and will eliminate the all-consuming task of positional cloning after QTL localization. Thus, as they relate to QTL regulating germinability, genes in *Arabidopsis* and rice will be the first targets. Once germinability QTL are cloned from these systems, researchers can take advantage of collinearity in related genomes to identify and clone candidate genes from other plant species.

As a caveat to this exciting scenario, not all loci in less well-characterized species will be orthologous with those that regulate germinability of rice and *Arabidopsis.* Moreover, other species may have unique genes that regulate germinability. For example, wild oat displays embryo dormancy, but embryo dormancy has not been clearly demonstrated in rice. Given the fact that there are about 250,000 species of flowering plants, it is likely that there will be many mechanisms regulating germinability of seeds. Understanding the environmental effects and interactions with mechanisms regulating germinability in weeds will present us with many future challenges.

Conclusion

Identifying mutant stocks and cloning QTL that regulate germinability are not ends unto themselves. Characterizing the genes (and their products) that regulate germinability using a variety of molecular, biochemical, biophysical, and physiological approaches will undoubtedly help elucidate mechanisms, biochemical pathways, and signal transduction cascades that regulate dormancy, afterripening, and germination. Fundamental knowledge about a characteristic of weeds like seed dormancy can be used to devise new and improved weed management strategies. New knowledge to apply toward such strategies will always be necessary because new problems continue to develop through the movement of invasive plants into new ecosystems and the adaptation of weeds like wild oats to current management practices (e.g., herbicide resistance) (Beckie et al. 1999; Buhler et al. 2000; Jana and Naylor 1982).

Sometimes we are faced with the challenge of determining how we might use dormancy genes or knowledge about dormancy genes in a management strategy. Here are some possible scenarios. Just as plant breeders seek molecular markers for marker-assisted selection for resistance to preharvest sprouting, weed ecologists might perform marker-assisted modeling to improve prediction of seedling emergence or population shifts in germinability due to management practices (Jana and Thai 1987; O'Donovan et al. 1999). In the vein of "if you can't beat them, avoid or join them," we might help plant breeders develop crops like "dormoats" that could be planted in the fall and emerge early in the spring (Burrows 1970). Fall planting with fall and winter dormancy would allow plants to emerge earlier in spring and thus to avoid competition from weeds and diseases. Last but not least, collaborative efforts might be made to engineer a soil microorganism to produce substances that act to stimulate germination (e.g., GA) or to engineer a seed-borne virus with genes or antisense genes that, in a species-specific manner, promote or reduce germinability. We hope imagination is our only limitation to the use of new knowledge on the biology of weeds to improve weed management.

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